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STUDIES IN THE TAXONOMY AND DISTRIBUTION OF THE EASTERN NORTH AMERICAN SPECIES OF LOBELIA

ROGERS MCVAUGH

(Plates 435 and 436)

THE present paper is intended as a study of the distribution of the species of *Lobelia* native to the eastern part of North America, with a view to establishing better understanding of the relationships within the group, the possible origin of the various species, and the relation of this group of species to the world-wide genus *Lobelia*. Early in the study it became clear that the identities of various species were much in doubt, which necessitated considerable taxonomic work, in an effort to clarify the situation so that significant distributional studies could be made.

Most of the work has been carried on at the Botanical Laboratory of the University of Pennsylvania during the years 1933–1935. Two summers have been spent in this time in eastern New York, largely in botanical studies, so that the writer has been able to gain acquaintance with all the northeastern species in the field. The remaining species have been studied only from herbarium material.

During the course of the project about 7000 sheets of dried material have been examined. This has been made possible through the generosity of the following gentlemen, to whom the writer wishes to express his sincere thanks: Dr. R. M. Anderson, National Museum of Canada, Ottawa, Can.; Dr. W. C. Coker, University of North Carolina, Chapel Hill, N. C.; Dr. E. L. Core, West Virginia University, Morgantown, W. Va.; Mr. C. C. Deam, Bluffton, Ind.; Dr. J. H. Ehlers, University of Michigan, Ann Arbor, Mich.; Dr. N. C. Fassett,

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HISTORICAL INTRODUCTION

The genus *Lobelia* was unfamiliar to the early European botanists, as only two species are represented in Europe, and these are widely dissimilar in appearance, and not co-extensive in their ranges. It is not until the second half of the 17th century that related species of the genus are consistently grouped together.

The first mention in literature of a species of *Lobelia* appears to be

that made by Charles l'Ecluse (Clusius) in 1611 (*10*). This is a description of *L. Dortmanna* L., and is copied verbatim by Ray (*61*).

A North American *Lobelia* is brought to attention by John Parkinson in 1629 (*51*); he had plants of *L. Cardinalis* L. from France, which had come originally from the St. Lawrence valley. No distinction is made by the early writers between this species and the Mexican *L. splendens* Willd. and *L. fulgens* Willd. (cf. Hernandez (*27*)).

By the end of the 17th century the campanulaceous affinities of *Lobelia* had come to be well recognized: in 1623 Bauhin (*4*) had included *L. urens* L. among the Mustards, but in 1686 Ray (*60*) places all the Lobelias known to him (except *L. Dortmanna* L.) under Rapunculus, which included most of the *Campanulaceae*. Moreover, Plukenet (*53*) distinguishes *Lobelia* (*Rapunculus*) from the rest of the *Campanulaceae*.

The greatest advance in classification, before Linnaeus, is made by Tournefort (*73*), who defines sharply the genus *Rapuntium*.

The name *Lobelia* is first used by Plumier (*54*) for a related genus, *Scaevola* L. Plumier dedicates the genus to Matthias de Lobel (1538–1616), the Flemish doctor and Botanist to James I of England.

After Plumier's use of the name *Lobelia*, it is taken up by Linnaeus for the genus known by the name at the present time (*35–41*).

General Discussion

As understood today, the genus *Lobelia* comprises between 200 and 250 species, widely distributed. The great majority (nearly 9/10) of the named species are native to Australia and South and Tropical Africa, with a large number in South and Central America and Mexico, as well as the Pacific Islands. Several species are found in China and eastern Asia. The genus is represented in western Europe by two species, and is absent from the rest of the northern Eurasian continent except in the extreme east. The North American Lobelias, as treated in the present paper, consist of 27 named species and varieties.

In summarizing, it may be seen that *Lobelia* is largely a genus of the Southern Hemisphere. The same may be said in general of the whole group *Lobelioideae*. Bentham (*5*) (1875) makes the following speculations:

"That the primitive race (a hypothetical ancestor of the whole family Campanulaceae) flourished very early in some region in con-

nexion with Africa. That the Lobeliae were first developed at a time when the geological or other conditions afforded some general means of communication between South Africa and Australia, between Australia, New Zealand, and Antarctic America, between South Africa and extratropical South America." These speculations were made largely because of species or genera common to New and Old Worlds. In addition, Bentham says,

"From thence (the place of origin in the Southern Hemisphere) Lobeliae appear to have spread in several distinct directions into and beyond the tropics, without any transverse northern connexion between the several lines."

It should be pointed out here that too much stress must not be laid upon such evidence as the above, in determining the origin of the North American species, for the following reasons: In the first place, the genus as a whole is evidently highly advanced from an evolutionary standpoint, as shown by the structure of the flower and fruit. Some authors have assumed that the ancestors of the highly advanced *Compositae* must be sought among the *Lobelioideae* (Delpino (*13*); Small (*68*)). Secondly, the world-wide distribution of the various species, combined with the great diversity of vegetative structure, types of inflorescence, types of seed coats, and flower color, points to the conclusion that the group has enjoyed a long evolutionary, or geological, history.

Rock (1919), in his monograph (*63*) of the Hawaiian *Lobelioideae*, says, in speaking of the Hawaiian genera,

"That their age is enormous and that they form with the Compositae the oldest element in our flora may be judged from their numerous species and their distribution over the whole group. . ."

The present writer hopes to show later that several of the North American species are in an old or decadent condition, which is favorable to the assumption of a great age for the genus as a whole.

If it be granted for the moment that the genus actually is a relatively old one, it is logical to assume that groups of species in various parts of the world may have arisen from several sources, which have now disappeared. In other words, two species geographically contiguous at present may have come from two widely separated ancestors, both of which have died out in the intervening geologic time.

This situation seems to be the one now existing in North America; the species here designated as "North American" (*Eulobelia* and *Hemi-*

pogon, in part, of Bentham and Hooker (*6*) (1876)) form a distinct group, apart from the Mexican and South American species, some of which occur naturally or as weeds in Florida, Texas, New Mexico and Arizona. Aside from purely structural characters, most of the species native to the United States and Canada may be shown to have characteristic geographical ranges and probable points of origin which definitely relate them as a group, and separate them from the tropical species now native in Mexico and southward.

The North American Lobelias were included by Bentham and Hooker in their "Genera Plantarum" (*6*) in two sections of the genus, *Eulobelia* and *Hemipogon;* the first of these all North American (except the east-Asiatic *L. sessilifolia* Lamb.), distinguished by the large short-pedicelled flowers in lax terminal racemes; the section *Hemipogon* including species of Europe, Africa, America and Australia, characterized by slender, simple or branching stems and few flowers. These divisions of the genus now seem somewhat artificial. Apparently no adequate classification can be devised, if based upon habit and appearance alone.

Characters used by earlier taxonomists as natural ones, and as criteria of affinity, such as pubescence of the anthers, or the presence or absence of tufts of bristles, seem to be of no great absolute value. The same may be said of the shape of the capsule, which may vary considerably in the same species. The writer has been able to find one character only, by which to separate the North American species from those of other geographical areas: the mature seeds of this group are peculiarly foveolate-reticulate, some more than others, according to species, and indicating several distinct lines within the limits of the group. The seeds of *L. sessilifolia*, which was formerly included in the section *Eulobelia*, are smooth with prominent wings, while the seeds of apparently related Mexican species such as *L. gruina* Cav., *L. fenestralis* Cav., and the tropical *L. Cliffortiana* and its relatives are perfectly ovoid, smooth and shining. No Mexican, Central American or West Indian species seen by the writer has a type of seed even approaching the roughened ones of species of the United States. It is of course obvious that a single character, however fundamental, is never wholly trustworthy in determining relationships. It seems, nevertheless, that an entirely consistent feature such as the above, in conjunction with the evidence from geographical distribution, points to a common origin for our species. Any connection with

an ancestor in the Southern Hemisphere, such as that suggested by Bentham (*5*), must have been very remote in time and before the development of our present forms.

DISCUSSION OF GEOGRAPHICAL DISTRIBUTION OF SPECIES

The region under consideration is mostly eastern North America, west to the Mississippi Valley; two species of *Lobelia* cross the continent, north of the moraine, and will be considered separately in detail; phases of *L. siphilitica* and *L. spicata* push westward to Colorado and Saskatchewan, respectively; *L. Cardinalis* and its very close relatives occur west to California and well south into Mexico. With these exceptions, all the forms concerned are confined to the eastern half of the continent.

In the first place, it is necessary to consider briefly the geological history of the area in question. During Cretaceous time the general land level in eastern North America was lower than at present, so that the present Coastal Plain was submerged, and the shore line followed the present (*16*) "Fall Line," which runs through New York, Philadelphia, Washington, Richmond, cuts off the eastern third of North Carolina, passes through Columbia, S. C., Augusta and Columbus, Ga.; swings west and north in Alabama, leaving about two-thirds of the state in the Coastal Plain; follows the course of the Tennessee River north to its mouth; passes across southern Illinois and southeastern Missouri; southwesterly through Arkansas, leaving about half the state below it; cuts off the southeastern corner of Oklahoma and passes southward near Fort Worth, Austin and San Antonio.

Upon the elevation of the Appalachian system and emergence of the Coastal Plain, a considerable area was thus thrown open for colonization by plants. We need consider no earlier major geologic changes, since existing species were not then represented on the earth; the only other factor that must be taken into account is that of glaciation.

The latest (and in eastern North America the best marked and usually most extensive) glacial period was in Pleistocene (Wisconsin) time, ending roughly 35,000 years ago. The terminal moraine (*2*) reaches from Nantucket across Long Island to Pennsylvania, southern Ohio, Indiana, and Illinois, then north to Minnesota and west roughly along the 48th parallel. It was formerly held that all land north of this line was covered by a solid sheet of ice, and that all plants now living in this area had migrated from south of the moraine since

Wisconsin time. It has been shown recently, however, by Fernald and others (*11*, *17*), that certain areas, such as parts of Newfoundland, were wholly untouched by Wisconsin ice, and students of phytogeography, as well as glacial geologists, are coming more and more to believe that such places as the Bruce Peninsula represent examples of (perhaps much more numerous) tongues of land which were partially unglaciated. If such be the case, many Canadian plants may have persisted in these areas during the ice invasion.

Of the 27 species and varieties here considered, nine are, so far as known, confined to the Coastal Plain, and one reaches above the Fall Line only into the prairies of Arkansas and Oklahoma. Two species (*L. Dortmanna* L. and *L. Kalmii* L.) are northern, and reach non-glaciated country only rarely. The remaining fifteen plants comprise ten rather distinct entities all of which are found in the Appalachian region of the eastern United States (although not necessarily confined to it), and five varieties, which, if not found in the Appalachian region, are clearly derived from the species found there.

The case of the two northern species may be discussed first. *L. Dortmanna* and *L. Kalmii* are clearly very distantly related to other American species, and to each other. The former differs from all other species by the combination of the scapose habit and hollow linear leaves; corolla smooth and slit only part way to the base; anthers all tufted; pedicels ebracteolate and seeds dark, with prominent square base. *L. Kalmii* also differs from all other species, having rather large, smooth flowers, in loose racemes, pedicels bracteolate in the middle, and very finely reticulate, acute-fusiform seeds. Both species are found, in suitable habitats, north of the moraine, from Newfoundland to British Columbia. The former is found also in western Europe (Great Britain, western France, Belgium, Denmark, northern Germany, western Russia, and Scandinavia, as far north as 68°, according to the Illus. Fl. Mit.-Eur. (*26*)); the European and American forms are apparently identical.

All theories as to the origin of these species must remain largely theories only. The modern range of *L. Dortmanna* suggests a circumpolar range in pre-glacial times. The extremely rare occurrence, both of *L. Kalmii* and *L. Dortmanna*, south of the glacial moraine seems to point to a survival within the glaciated area, rather than south of it; however, the scarcity of suitable habitats such as calcareous bogs and sandy ponds in unglaciated country may account for the distribution.

Whatever the explanation of the above, it is sure that any past connection with the remaining species is very remote.

With the exception of the two species just considered, the group as a whole is rather uniform in character and rather closely related, although divisible into the following sub-groups:

a) Species with a smooth lip, small flowers, delicate stems; in Piedmont, Mountains and northeastern Coastal Plain represented by *L. Nuttalli;* this giving way in Florida to *L. Feayana,* which is not surely separable from it by any one character.

b) Species with larger flowers, usually in spikes, a hairy lower lip to the corolla, and an entire corolla-tube (except for the dorsal slit). This is the *L. spicata* complex, which has apparently given rise to *L. inflata, L. Canbyi,* and possibly to *L. Boykinii.*

c) Two species very close to the above, but with characteristic thin and smooth leaves, and secund racemes: *L. Gattingeri* of the uplands of Tennessee, giving way in the Coastal Plain to *L. appendiculata.*

d) Four species evidently related to the last two, but with a tendency to reduction of the stem-leaves, and to a fenestrate corolla (one in which the two upper petals have separated from the corolla-tube near the base): *L. flaccidifolia, L. Halei, L. floridana, L. paludosa.*

e) Large, coarse, smoothish species with showy flowers, the corolla with a smooth lip, fenestrate: the seeds roughly ridged and long rather than ovoid; *L. Cardinalis, L. siphilitica, L. amoena, L. elongata,* possibly *L. glandulifera.*

f) Coarse species with large flowers, fenestrate corolla, smooth lip. Seeds rather small, smoothish, ovoid, resembling those of *L. spicata* and its allies: *L. puberula* and its forms. From a form like *L. puberula* may have come the two species *L. brevifolia* and *L. glandulosa.*

The sub-groups may now be discussed in detail:

a) Inspection of the maps (FIGS. 27 and 28) will show the apparent relations: *L. Nuttalli* or its immediate ancestor seemingly migrated in post-Cretaceous times, southeastward onto the emerging Coastal Plain, where it gradually extended its range both northeastward and southward. It did not enter the Florida peninsula, but gave rise there to the rather similar *L. Feayana.*

b) In the Appalachian and Ozark regions the dominant representative of this sub-group is *L. spicata* var. *leptostachys,* which is not found elsewhere, except on the immediately adjacent portions of the Gulf Coastal Plain (FIG. 14); it is not found on the Atlantic Coastal

Plain, being there in part replaced by the var. *scaposa* (FIG. 18); in the northeastern states, west to the Great Lakes, it gives way to the var. *originalis* and the var. *campanulata* (FIGS. 15 and 17). Westward and northwestward, from Illinois and Missouri, the var. *hirtella* appears (FIG. 16). Where the ranges of these varieties overlap, a host of intermediates is found. These cannot be referred with certainty to any of the named forms, and constitute the best reason for reducing *L. leptostachys* from the rank of species, and for postulating that it or a plant similar to it may have been the ancestor of all the varieties of this sub-group (FIG. 19).

It is unfortunate for the sake of clarity that the rules of priority make the northeastern *L. spicata* Lam. the type of the species, for it seems to have been derived from the var. *leptostachys* by the disappearance of the auricles (which sometimes reappear in individuals) and by adaptation to a somewhat more mesophytic habitat. Accordingly, it seems best to refer the northeastern phase to var. *originalis*. The var. *hirtella*, on the other hand, may have arisen from the var. *leptostachys* in a more xerophytic habitat.

Of the three remaining members of this sub-group, *L. Canbyi* is not separable from the *spicata* complex by any character of the corolla; its seeds are almost exactly similar, also. It has seemingly spread from the Appalachian region to the Atlantic Coastal Plain (FIG. 21). *L. Boykinii* is a rather distinct species of the Atlantic Coastal Plain, whose affinities are obscure; it resembles no other species very closely, and seems to approach *L. Canbyi* only through the habit and the slightly hairy lip (FIG. 22).

The final species, *L. inflata*, is very distinct, but seems to show its connection to the *spicata* complex by the spicate character of the young inflorescence, the hairy lip, the seeds, which are very similar to those of *L. spicata* and varieties. It is possible that some connection may be shown through the reduced number of flowers and the subinflated capsule of *L. spicata* var. *campanulata*, but this is only a speculation. *L. inflata* evidently has spread from the Appalachian region; it has, however, been unable to enter the Coastal Plain very extensively (FIG. 20).

c) Logic similar to the above would demand that *L. Gattingeri* be an ancestral type, and have given rise to *L. appendiculata* (FIG. 23). However, the range of the former is so restricted that such a conclusion is largely guesswork; with the reservation that, as stated

elsewhere, the two are difficultly separable in the final analysis other than through geographic range. It would seem to be taxing the power of coincidence to postulate two forms having had exactly parallel development, but no relationship. This is especially true in such a region as the one under discussion, where the evidence seems to be for development away from the Appalachian region, in radial directions.

d) On the southern Coastal Plain occurs this sub-group of four species. They show their relation to *L. Gattingeri* and *L. appendiculata* by a tendency to develop auricles, and by the characteristic bell-shaped capsule. They show their connection to sub-groups (b) and (c) by the spicate habit and the hairy lip. Two of the species, *L. flaccidifolia* and *L. Halei*, of the southeastern and southwestern Coastal Plains, respectively, are set apart by the large, usually green bracteoles near the middle of the pedicels (It is possible that *L. flaccidifolia* is only a habitat form: cf. discussion under this species). Both show an increase in flower size from the *spicata* complex, and there is a tendency for the corolla to become fenestrate. The leaves in *L. Halei* (FIG. 24) may be rather bunched near the base of the stem, as is sometimes seen in *L. spicata* var. *hirtella*.

In *L. floridana* this reduction of leaves has gone further, so that they are nearly all basal; the prominent auricles of *L. Halei* have vanished, and the bracteoles are inconspicuous. This is a species mostly (so far as known) of the Gulf States, from west Florida westward along the coast. It is also known from Wilmington, N. C. (FIG. 25).

Apparently the most advanced of this sub-group is *L. paludosa*, which has developed in peninsular Florida, and west about to the Apalachicola River. The leaves are entirely basal, there are no bracteoles on the pedicel, and the corolla has become plainly fenestrate (FIG. 26).

e) This sub-group is a rather composite one, based in part upon the patently artificial character of size; the species seem, however, to agree well in seed characters (PLATE 435).

In the first place, *L. Cardinalis* is a wide-spread species, very different in form of flower, as well as in color, from other North American ones; its color suggests Mexican affinities (although parallel development in the case of color is not by any means rare), as does the fact that it is represented throughout the Southwest by the plants passing as *L. splendens* Willd. (FIG. 4) and *L. fulgens* Willd. Its recent spread in this country may well have been, nevertheless, from the Appalachian region, where it is now common (FIG. 3).

The second species, *L. siphilitica,* is abundant in the Appalachian region, but has not spread to any extent into the Coastal Plain, nor far northeast into glaciated country. It has, however, migrated westward as the var. *ludoviciana* (FIG. 6), as far as Colorado. In Wisconsin and Minnesota, southward through Missouri, many intermediates appear; the typical form is not uncommon in the Ozark region (FIG. 5).

What passes for *L. amoena* Mx. is a much misunderstood plant of the Appalachian Mountains and Piedmont (FIG. 7). Small (*71*) gives this as a Coastal Plain species, which is obviously an error, probably based upon the misidentification of plants of *L. glandulifera* from Florida. The species itself is confined to the uplands, but the closely related *L. elongata* has developed in the eastern Coastal Plain (FIG. 8). The position of *L. glandulifera* Small is not wholly clear: it combines the flower-size and glandular calyx-lobes of *L. glandulosa* with the smooth corolla and general smoothness of *L. amoena.* The capsule is intermediate (where seen) between those of *L. amoena* and *L. puberula.* It seems best to regard it as a distinct species, close to *L. amoena,* perhaps also related to *L. glandulosa.* Its range is both Appalachian and Coastal Plain (FIG. 9).

f) *L. puberula* is separated from the species in the preceding subgroup because of the seeds, which seem closer to those of the *spicata* complex (PLATE 435). It has (in one of its phases) an Appalachian range (FIG. 12), almost identical with that of *L. spicata* var. *leptostachys.* This is evidently the ancestral type; it grades freely into several forms: one on the Atlantic Coastal Plain (FIG. 13), in which development has been in the direction of a hirsute calyx, large and leafy bracts, broad calyx-lobes and obtuse leaves. Southward the species becomes nearly smooth (Alabama, Mississippi); from Florida little material has been seen, but it seems to approximate the Appalachian type or that of the Atlantic seaboard. Westward and southward (Louisiana, Texas, to Arkansas) the species grades into the form with strongly dentate leaves, large long bracts, but rather smooth calyx. In other words, the Appalachian or central type of *L. puberula* seems to pass into several forms which radiate, as it were, from a central one.

The two remaining species, *L. brevifolia* and *L. glandulosa,* are closely related to each other, as shown by flower-structure. The common ancestor, if any, is, however, very much in doubt. The most

probable suggestion seems to be that both have been evolved from a plant related to *L. puberula;* all have a similar type of pubescence on the calyx, besides the fact that a number of plants have been seen which resemble hybrids of *L. puberula* and *L. brevifolia,* which may indicate relationship.

PROBABLE RELATIONS OF SPECIES

It seems well at this point to discuss the features of this part of the genus *Lobelia* which seem important as indicators of relationship, as well as those characters which appear to be primitive or advanced.

A. INDICATORS OF RELATIONSHIP.

1. Seeds. So far as can be determined, this is the most important single character. Species like *L. Kalmii* and *L. Nuttalli,* which were confused by the earlier botanists, and considered closely related, are separated by several good characters and are evidently not very closely connected. The seed-differences alone, in this case, are so striking as to make this obvious (PLATE 435).

2. Pubescence of Corolla. The loose or dense mat of hair at the base of the lower lip in many species, considered in conjunction with other corolla-characters, is often of great help in taxonomy of the group. For example, *L. Canbyi,* long considered close to *L. Nuttalli* because of similar habitat and manner of growth, has the hairy lip and flower-structure of the *spicata* complex.

3. Other Corolla-Characters. Size of corolla is a weak character, in general, as is the degree of external pubescence; this applies as well to the size and degree of pubescence of the stamens. However, the lengths of the corolla, anther-tube, and filament-tube are all very constant in the same species within small limits, and often serve as good specific indicators when used with other characters. Fenestrate corollas have appeared separately in several groups (including the Mexican *L. fenestralis* Cav.), so that this is of general importance only.

4. Calyx-Characters. General shape of calyx and degree of inferiority of capsule are of considerable importance, but too much stress should not be placed upon them, as they vary even between different flowers of the same plant. The general form of the calyx-lobes is to be considered, but their length is very variable (width also), and the presence or absence of glandular teeth is not a constant character. The presence of auricles at the base of the calyx-lobes is

evidently an ancestral character which has persisted without any apparent correlation with other features.

5. Pubescence. The absolute amount of pubescence present is so variable in the same species that it makes little difference, but the character of this pubescence is in some cases important. For example, in the sub-group of *L. spicata* and its relatives, the base of the stem is densely short-pubescent. In some forms of *L. puberula* there is found very nearly the same type of hairiness, which is further evidence of the relation suggested by similarities in range and in seed-characters. Furthermore, certain plants found in Arkansas and Oklahoma are to be distinguished from *L. spicata* only by the fact that the stem is slightly hirsute in lines only, just as in *L. appendiculata.*

6. Leaf-Characters are so easily influenced by environment that they are relatively of little importance. The best example of this is furnished by *L. Kalmii*, in which the leaves vary from linear-filiform to broad elliptic, depending on the habitat.

7. Inflorescences and Branching. Most of our species have a definite central axis with subordinate lateral branches, but the degree of branching is sometimes helpful.

B. ADVANCED OR PRIMITIVE CHARACTERS.

1. Plants with leaves all cauline are considered more primitive in this respect than those with basal rosettes only; the latter all possess vestigial cauline bracts, which in some cases develop into leaves.

2. The same reasoning applies to the bracteoles usually found on the pedicel. It seems logical to assume that they are the remains of more or less leafy bracts, and are gradually disappearing; this is confirmed by their absence in such highly specialized species as *L. Dortmanna* and *L. paludosa.*

3. The Occurrence of Auricles. In general, this is probably a primitive character, in respect to this group. This is confirmed by their presence in forms like *L. spicata* var. *leptostachys, L. puberula,* and *L. Halei,* and their subsequent loss in related and obviously derivative plants such as *L. spicata* var. *originalis, L. floridana,* etc.

4. Separation of Petals from the Corolla-tube. The condition of a "fenestrate" corolla seems to be an advanced one. If, as is now mostly accepted by taxonomists, freedom of flower-parts is a primitive condition, then the corolla-tube of *Lobelia* must have come from once separate petals. It is hard to see how the fenestrate condition could have arisen without the tube once having been entire (FIG. 1). The

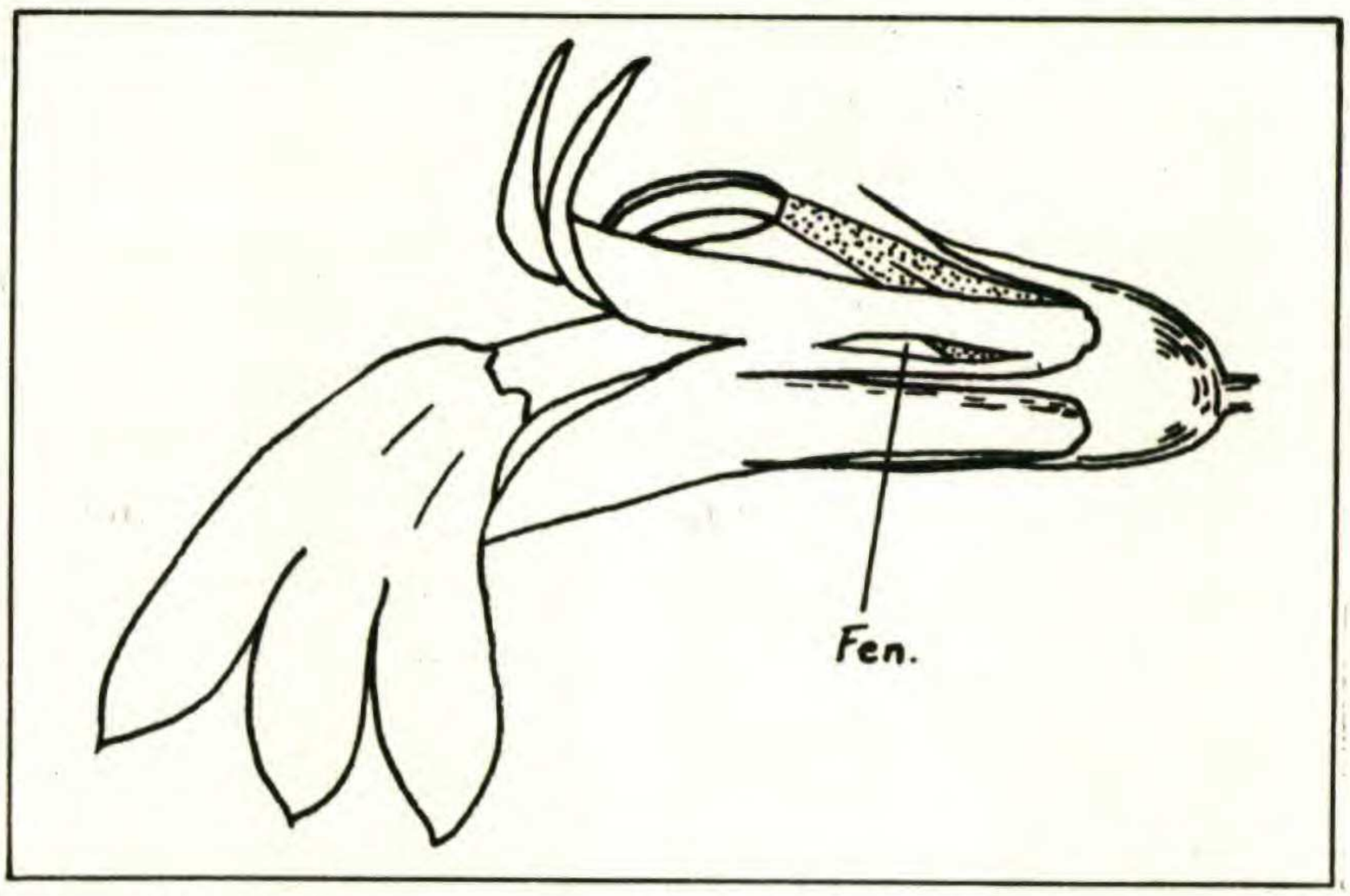

FIG. 1. Flower of LOBELIA, showing Fenestration.

same is true for the filament-tube, but this has split apart at the base in all the species, so that it is of practically no use as a taxonomic character.

5. Size. Larger flowers are probably, but not necessarily, usually more advanced; the large-flowered group shows more diversity in form of flowers than do the others, and is usually accompanied by a fenestrate corolla, both of which features indicate advance.

With the above statements in mind, as well as the geographical evidence already presented, we are able to visualize a possible ancestral plant which existed in North America in Cretaceous or early Tertiary time, probably in the region of the southern Appalachians. As a matter of fact, there may have been several ancestral types: excluding *L. Dortmanna* and *L. Kalmii*, which were apparently separated from the rest of the group much earlier, there are two main lines, which may be designated roughly as the small-flowered and the large-flowered.

In the latter, *L. Cardinalis* is a distinct individual, and has perhaps existed unchanged since Tertiary times. The same may be said of *L. siphilitica*, while *L. amoena*, *L. elongata* and *L. glandulifera* may well have come from a common ancestor.

The small-flowered species seem to have come from a plant with flowers near those of *L. spicata* in size, non-fenestrate corolla with hairy lower lip, single racemose inflorescence, auricles on the calyx-lobes, and broad, cauline leaves. This early diverged into two lines; one of these developed large flowers and a fenestrate corolla, without

the hairy lower lip (*L. puberula* and its allies). This line is a possible source of *L. glandulosa* and *L. brevifolia*. The second line failed to

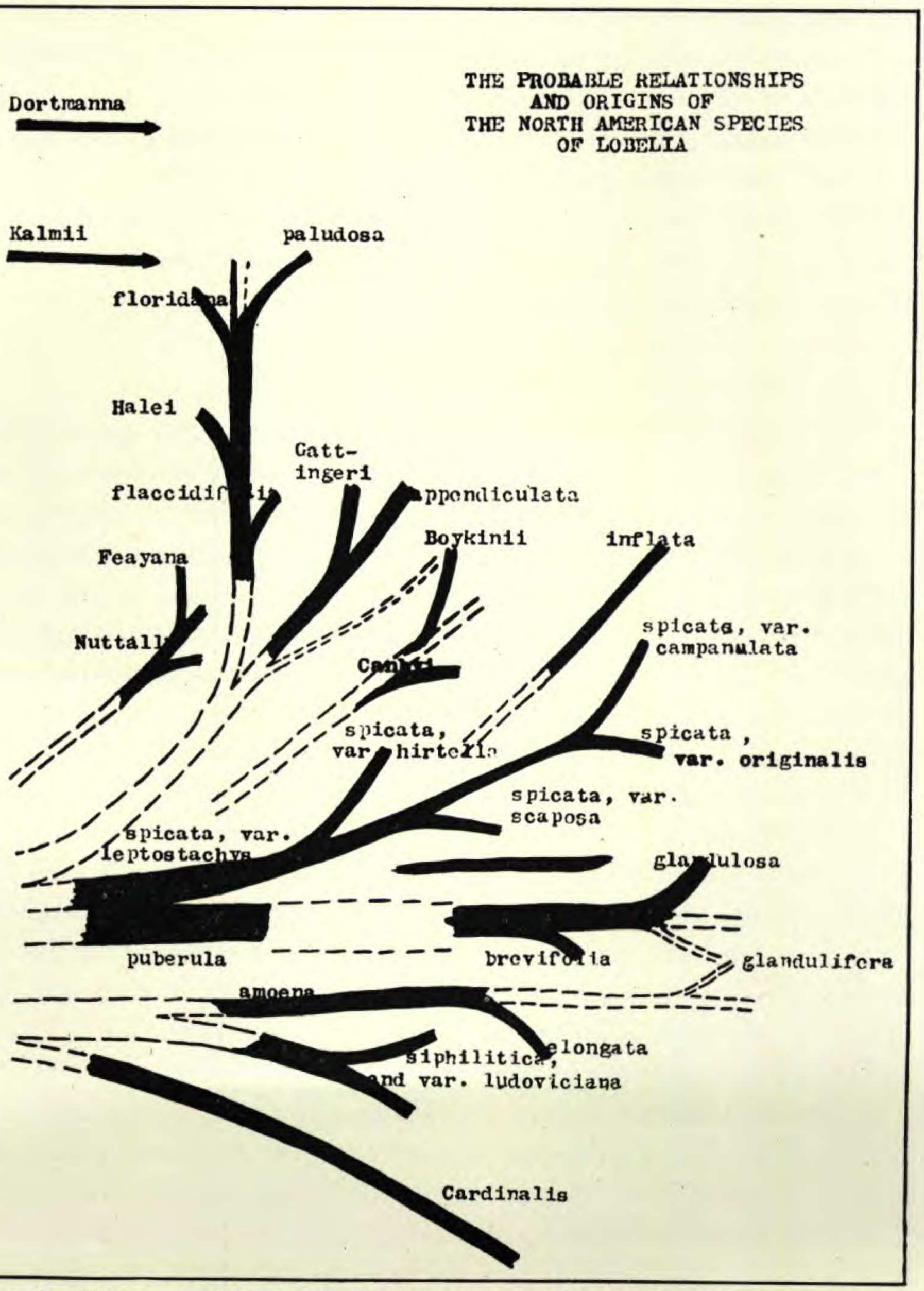

FIG. 2. Diagram of Probable Relationships of North American Species of LOBELIA.

develop large corollas, but branched out in several ways (FIG. 2). The forms of *L. spicata* make up one branch, a second being formed by

L. Gattingeri and *L. appendiculata*. A third branch is that culminating in *L. paludosa*. The line of *L. Nuttalli* and *L. Feayana* shows some resemblances in leaf and capsule to *L. spicata*, and very possibly is a minor offshoot of this complex.

Further evidence for the above, although not wholly satisfactory, is afforded by the fact that supposedly older types, such as have given rise to wide-ranging varieties and species, are confined in several cases to restricted ranges; they are not aggressive. It may be that such plants as *L. Gattingeri*, *L. amoena*, *L. spicata* var. *leptostachys*, and the Appalachian representative of *L. puberula* are old species which have passed the colonizing stage of their existence.

GENERAL CONCLUSIONS

The partly unsupported conclusion reached in this paper is that from one or more ancestral types living in the Appalachian region of the Southeastern United States, in Tertiary time or before, have come a majority of the species of Lobelia now native in this region. Secondly, that these changes have been brought about by the natural radial spread of the original species, so that closely related plants are seen to be occupying different radii of the same hypothetical circle. These relatives are usually not to be considered cases of simple linear development, but of parallel development from a common ancestor. There are several excellent cases in point:

1. The western var. *hirtella* of *L. spicata* did not come from the var. *originalis* of the eastern states, as has been assumed, but from a plant like *L. spicata* var. *leptostachys*, in a central position (*cf.* FIG. 19).

2. The Appalachian phase of *L. puberula* is replaced in the East by one derivative, and in the West by a similar but distinct one, both of which must have come from the first, as neither of the outlying ones, so far as known, occurs in between (*cf.* FIG. 20).

3. On the Coastal Plain of Florida and Georgia, west about to the Apalachicola River and the eastern edge of Alabama, occur three species; *L. glandulosa*, *L. paludosa*, and *L. flaccidifolia*. West of this line, their places are taken quite abruptly by *L. brevifolia*, *L. floridana*, and *L. Halei*, respectively: taken in each case by a closely related species. Wherry, in a geographical study of the southern Sarracenias (Mss.), finds somewhat the same situation in that genus, and assumes that these related forms have come separately from a common ancestor, along one of the many more or less parallel streams leading

out of the Appalachian region to the Coastal Plain (FIGS. 10 and 11. *cf.* also FIGS. 24, 25, 26).

In the foregoing the writer has attempted to show that the North American Lobelias form a distinct unit, clearly separable from geographically neighboring ones. It is true that the conclusions reached here are largely theoretical, but in reaching them every effort has been made to stay within the bounds of evidence actually at hand, and those of logic.

In the following pages is given a conspectus of the North American species, with detailed data of the plants themselves, and their ranges. No attempt has been made to give the complete synonymy for all species; only the most important references are included.

In citing herbarium specimens, one record only is given for each county, except in special cases such as large counties or districts, little-known species, or areas near the limits of ranges. For the wide-ranging and well-known species *L. Cardinalis* L., *L. siphilitica* L., *L. inflata* L., *L. Kalmii* L., and *L. Dortmanna* L. a few citations only or dots on the maps are given for each state or province. For all other species and varieties, at least one record is given for each county or district where the plant is known to have grown. Near the edges of the ranges of the above five species, all known county records from certain states have been given; in such cases the citations from that state are followed by (ALL).

All other things being equal, specimens with collection-numbers have been cited; likewise, those which are represented by duplicates in several herbaria. Except where noted, the ranges given at the ends of the descriptions of species have been compiled only from material actually seen.

CONSPECTUS OF THE NORTH AMERICAN SPECIES

LOBELIA [Plumier] Linnaeus, Gen. Pl. 897. Ed. V. 401. 1754.

Type Species: *L. Dortmanna* L., Sp. Pl. II: 929. 1753. This is chosen as the type because it was the species best known to Linnaeus in Sweden, and was mentioned in the "Flora Lapponica."

Not *Lobelia* Plumier, Gen. 21. 1703; plate 31. (=*Scaevola* L.).

Dortmanna [Rudbeck] Linnaeus, Syst. Ed. I. 1735 (fide Index Kew.).

Lobelia Linnaeus, Gen. Pl. Ed. I. 267. 1737.

Rapuntium Tournefort, Inst. R. H. 163. 1700. Presl, Prodr. Mon. Lob. (1836).

Our species annual or perennial herbs, with acrid milky juice con-

taining more or less of an alkaloid, lobelin; leaves alternate, simple, exstipulate, usually with callose-glandular teeth. Pubescence variable, greatest near the base and near the margins of the leaves; pedicels usually pubescent or rough-puberulent. Inflorescence racemose or paniculate; usually with a main axis, and branches, if any, subordinate and developing later. Flowers perfect, 5-merous, red, purplish or blue to white; calyx-tube persistent, adnate to the ovary; corolla irregular, inserted with the stamens just where the calyx becomes free from the ovary; the lobes of the corolla mostly valvate or induplicate in the bud, the tube slit to the base between two of them (in flower the two next the axis of the inflorescence; actually the two next the bract: the reversal of position is brought about by the twisting of the pedicel in anthesis). Two petals next to the cleft often separating incompletely from the tube, from below upward, making the tube fenestrate. Limb bilabiately irregular, the three (apparently) lower lobes spreading, more or less reflexed, usually broad; the two (apparently) upper erect or recurved, usually narrow and shorter than those of the lower lip. Lower lip hairy at base in some groups, often tuberculate at base. Pedicel usually with two bracteoles near the base or above it. Stamens as many as the lobes of the corolla and alternate with them, syngenesious and partially monadelphous; anthers 2-celled, introrse, united into a tube; the two (apparently) lower smaller, with a tuft of white hairs at the tip; the three upper larger, smooth, pubescent on the backs, or tufted at tip. Filaments flat, united above from half to two-thirds their length, usually hairy below; persistent, with the anthers, in fruit. Limb of the calyx divided down to the ovary, which is wholly inferior or sometimes nearly free; calyx-lobes entire or toothed (species with normally entire calyx-lobes may have individuals with dentate lobes); lobes often with appendages at the base. Ovary 2-celled, with axial placentae, loculicidally 2-valved. Style entire; stigma 2-lobed, with a ring of hairs below the apex. Ovules numerous, anatropous. Embryo small, straight, with copious fleshy endosperm. Seeds small, roughened, foveolate-reticulate.

27 eastern North American species and varieties.

In addition, the following species (or forms usually identified as such) occur in the southern and south-western United States; they are not considered in the present paper because the larger parts of their ranges are South or Central American. None except the last belongs to the group here designated as "North American":

L. Berlandieri A. DC., *L. Cliffortiana* L., *L. Cliffortiana* L., var. *brachypoda* Gray, *L. fenestralis* Cav., *L. gruina* Cav., *L. Xalapensis* HBK., *L. splendens* Willd.

ANALYTICAL KEY TO SPECIES

1. Flowers large, straightened out 18–45 mm. long, including calyx. Corolla normally fenestrate. Terrestrial or swamp plants with leafy stems. Seeds rough-tuberculate (2).
   2. Flower crimson (white forms occurring as sports), 30–45 mm. long, including calyx (3).
      3. Anther-tube 4.0–5.5 mm. long. Filament-tube 24–33 (usually 28–30) mm. long. Leaves lanceolate to ovate-lanceolate, three times as long as wide or less, 1.5–6.0 × 6.0–18.5 cm. Smooth or sparsely hirsute-pubescent. Plants of the eastern half of the continent ..... 1. *L. Cardinalis.*
      3. Anther-tube 3.5–4.5 mm. long. Filament-tube 19–23 (26) mm. long. Leaves lanceolate to linear-lanceolate, about seven times as long as wide, 0.4–3.0 × 5.5–21.0 cm. Smooth or sparsely pubescent. Plants of southwestern United States and Mexico ..... (1) *L. splendens.*
      (The related rough-pubescent *L. fulgens* Willd., of Mexico, has not been seen from the United States).
   2. Flowers blue or violet (white forms occurring as sports), 18–33 mm. long (4).
      4. Filament-tube 12–15 mm. long. Calyx-lobes with broad, leafy auricles at their bases (auricles ovate-obtuse to -acute, 2–3 mm. long, not glandular-dentate). Pedicels with a pair of conspicuous bracteoles just below the calyx or ⅓–½ the length of the pedicel below it (a).
         a. Whole plant more or less hairy. Calyx and its lobes hirsute. Inflorescence usually long and dense. Leaves broad-ovate or -lanceolate, 2–6 × 6–18 cm., irregularly toothed. Plants often tall (75–100 cm.). Eastern ..... 2. *L. siphilitica.*
         aa. Plant nearly smooth, usually 30–60 cm. high. Calyx and its lobes sometimes sparsely hirsute. Inflorescence shorter (6–20 flowers). Leaves smooth, lanceolate, about 1.5 × 6.0 cm., shallowly toothed or subentire. Plant of mid-western United States. ..... (2) *L. siphilitica*, var. *ludoviciana.*
      4. Filament-tube 6–11 mm. long. Pedicel with a pair of bracteoles at or near the base. Auricles of the calyx present or absent (5).
         5. Calyx-lobes (usually) prominently glandular-dentate or pectinate, never hirsute. Flowers few, 3–20 (27), in loose, secund racemes. Pedicel stout, in fruit usually stiffly upright (b).
            b. Calyx-lobes pectinately toothed. Auricles broad, leafy, round, fimbriate, nearly covering the hemispheric calyx. Leaves numerous, to 200, small, narrow, obtuse, to 0.5 × 3.0 cm., prominently denticulate. Flowers 6–20, 18–20 mm. long, hairy-strigose outside. Lower lip of corolla smooth or nearly so. Filament-tube about 7 mm. long ..... 7. *L. brevifolia.*
            bb. Calyx-lobes prominently glandular-toothed, or nearly entire. Auricles none or very small, triangular. Flowers large, 20–33 mm. long, smooth outside, the corolla-lobes about equaling the tube in length (c).

c. Plants usually weak; leaves 5–10, long-linear, to 0.5 × 15.0 cm., usually prominently denticulate. Flowers 1–10 (15), 20–33 mm. long. Lower lip of corolla hirsute at base. Filament-tube 8–10 mm. long. Calyx often chaffy-hirsute.....6. *L. glandulosa.*

cc. Plants slender or erect, smooth throughout. Leaves thick, lanceolate to oblong or ovate, to 3 × 7 cm., shallowly toothed or subentire. Flowers 6–20, 20–28 mm. long. Lip of corolla smooth. Filament-tube 7–8 mm. long....5. *L. glandulifera.*

5. Calyx-lobes (usually) entire, rarely with a few teeth, smooth or pubescent. Flowers 20–100 in often dense more or less secund racemes. Pedicels in fruit curved to one side (6).

6. Plants smooth or nearly so. Calyx-lobes narrowly linear-lanceolate, about 1 mm. broad, smooth. Auricles none or very small. Calyx campanulate in flower, becoming globose in fruit (d).

d. Leaves narrowly lanceolate, to 1.5 × 10.0 cm., acute, sharply denticulate. Filament-tube 8–11 mm. long. Anther-tube 4 mm. long. Calyx-lobes 6–13 mm. long. Species of the southeastern Coastal Plain.....4. *L. elongata.*

dd. Leaves lanceolate to broadly ovate or the lower elliptic, thin, shallowly crenate or subentire. Filament-tube 5–7 mm. long. Anther-tube 2.5–3.5 mm. long. Calyx-lobes 5–11 mm. long. Species of mountains and Piedmont, southeastern United States.....3. *L. amoena.*

6. Plants more or less short-pubescent throughout. Calyx-lobes lanceolate or broader, 2–4 mm. wide, 5–12 mm. long, ciliate-pubescent, usually more or less auriculate at the base. Calyx flat or turbinate in flower, becoming conic-hemispheric in fruit (e).

e. Flower-bracts usually leafy, broad-ovate, to 1.5 × 2.0 cm. Calyx usually densely hirsute-chaffy. Calyx-lobes broad at the base, ovate-triangular, to 4 × 12 mm., the edges much rolled back, especially in fruit, forming large rounded auricles. Leaves obovate-obtuse below, coarsely toothed, ovate above. Plant of Coastal Plain and adjoining territory, Ga. to N. J. In the region from Texas to Ark. and Mo. a similar plant with smoother calyx and strongly dentate leaves.....8. *L. puberula.*

ee. Flower-bracts lanceolate, 1–2 cm. long in the lower flowers. Calyx usually pubescent, sometimes glabrate (rarely hirsute). Calyx-lobes lanceolate, to 2 × 12 mm., little rolled at the edges, even in fruit. Auricles none, or small, triangular. Leaves 10–20, oblong, acute, or obtuse below, mostly sharply denticulate. Plant of uplands, Ohio to Ga. and westward. .....8. *L. puberula.*

1. Flowers smaller, 10–22 mm. long, including calyx. Corolla normally not fenestrate (or becoming so in a few southern species). Seeds rough-tuberculate. Terrestrial or aquatic (2).

2. Plants aquatic; leaves fleshy, linear, hollow, forming a

basal rosette. Scape nearly naked, few-flowered. Anthers all densely tufted at tip. Capsules long-stalked, pendent. Occurring north of the moraine.....22. *L. Dortmanna.*

2. Plants aquatic or terrestrial, leaves flat. Stems leafy or sometimes leaves nearly all radical (3).
   3. Plants with slender, more or less delicate stems and narrow leaves, seldom over 50–60 cm. high. Base of lower lip of corolla smooth (4).
      4. Flower 10–13 mm. long, calyx elongate, capsule ovoid. Pedicel with a pair of sub-opposite bracteoles about the middle. Plants of calcareous bogs and rocks, north of moraine.....21. *L. Kalmii.*
      4. Flower 7–10 mm. long. Calyx flat or conic. Bracteoles of the pedicel at its base (5).
         5. Plants 20–60 (75) cm. high, erect. Leaves lanceolate, the basal spatulate. Calyx flat; capsule hemispheric, half inferior, often bristly.....19. *L. Nuttalli.*
         5. Plants 10–30 cm. high, weak, decumbent. Leaves sub-orbicular and petiolate below. Capsule turbinate, acute at base, ⅔ or more inferior, smooth. Peninsular Florida.....20. *L. Feayana.*
   3. Base of lower lip of corolla densely hairy or rarely nearly smooth. Plants not delicate, often tall (75–125 cm.); usually not diffusely branched. Leaves broad or sometimes linear (6).
      6. Leaves linear-lanceolate or filiform, cauline rarely 0.4 cm. wide. Inflorescence loose, mostly branched (7).
         7. Pedicels and calyx smooth. Bracteoles of pedicel none. Usually much branched above; aquatic, with leaves often deciduous, flowering May-June. .....12. *L. Boykinii.*
         7. Pedicels and calyx scabrous. Bracteoles at base of pedicel. Simple or somewhat branched, leafy; not aquatic, but living in swamps. Flower August–October.....11. *L. Canbyi.*
      6. Leaves broad, seldom less than 1 cm. wide. Inflorescence not diffusely branched (except in *L. inflata*) (8).
         8. Calyx ovoid; capsules developing early, much inflated, ovoid, inferior. Usually much branched, especially in age. Stem usually long-hirsute...10. *L. inflata.*
         8. Plants never diffusely branched (sometimes with few subordinate side branches); inflorescence a terminal spike or raceme. Stem never long-hirsute. Capsules various, never much inflated (9).
            9. Leaves strap-shaped or oblanceolate, mostly basal. Bracteoles of the pedicel inconspicuous or none. Semi-aquatic or swamp plants of the Southern Coastal Plain (10).
               10. Plants tall, 80–100 cm. Filaments 7–9 mm. long, deflexed. Corolla-tube not fenestrate, but often with a thin place on each side of the wall. Pedicels with inconspicuous bracteoles.....17. *L. floridana.*
               10. Plants 50–60 cm. tall. Filament-tube about 3.5 mm. long. Corolla-tube fenestrate. No bracteoles visible on the pedicel.....18. *L. paludosa.*
            9. Leaves mostly cauline, or, if radical, broad-ovate,

petiolate. Terrestrial plants of wet or dry places (11).

11. Pedicel with two conspicuous green bracteoles about half way up. Auricles of calyx deflexed, round, small. Plants of the southern Coastal Plain (12).

12. Plant nearly unbranched, with thick oblanceolate or lanceolate acute leaves. Flower 19–20 mm. long, pubescent. Filament-tube 6–8 mm. long.....16. *L. Halei.*

12. Plant simple or branched, with thin oblong usually obtuse leaves. Flower 15–16 mm. long, nearly smooth; corolla-tube sometimes fenestrate; filament-tube 5–6 mm. long.....15. *L. flaccidifolia.*

11. Pedicels with bracteoles at base. Auricles various (13).

13. Stem-leaves thin, sessile with a broad base, short-ovate, nearly smooth. Basal leaves small or none. Stem nearly smooth, even at base. Raceme more or less plainly secund (14).

14. Calyx-lobes smooth; auricles none; central Tennessee.....14. *L. Gattingeri.*

14. Calyx-lobes strongly glandular-ciliate. Auricles glandular-ciliate, very small or larger, foliose, scarious-tipped...13. *L. appendiculata.*

13. Stem-leaves ovate or oblong to lanceolate, somewhat pubescent and narrowed at base. Stem densely short-pubescent below. Inflorescence a terminal unbranched spike, not plainly secund (15).

15. Basal leaves large, roundish, conspicuous; the cauline 1–5, very small, bract-like. Raceme loose, nearly half the height of the plant. Auricles of calyx evident, but not long-filiform....9e. *L. spicata*, var. *scaposa.*

15. Leaves mostly cauline; if basal, rarely roundish and usually with cauline leaves also present (16).

16. Plants strongly rough-pubescent, including stem, bracts, and the long calyx-lobes. Lower bracts leafy. Plants often short (20–50 cm.), with leaves low on the stem. Auricles small or none.....9c. *L. spicata*, var. *hirtella.*

16. Plants smooth or pubescent, leafy, often 50–100 cm. high (17).

17. Auricles long-filiform, deflexed, often as long as the calyx-tube. Inflorescence usually a dense narrow spike. Leaves oblong, more or less appressed. Plants sometimes ciliate.....9a. *L. spicata*, var. *leptostachys.*

17. Auricles very short or none. Plants usually smooth. Inflorescence a terminal raceme or spike, usually much less than half the height of the plant (18).

18. Anthers blue; calyx in anthesis flattish. Flower light blue. Raceme dense, many-flowered. Capsules short-hemispheric.....
.....9b. *L. spicata*, var. *originalis*.

18. Anthers white. Calyx in anthesis roundish. Flowers dark purplish-blue. Raceme few (10–30) -flowered. Capsules globose, often somewhat inflated.....
.....9d. *L. spicata*, var. *campanulata*.

(*To be continued*)

EIGHTH REPORT OF THE COMMITTEE ON PLANT DISTRIBUTION

The present report deals with the tribes *Oryzeae*, *Phalarideae*, *Agrostideae* and *Aveneae* of the family *Gramineae*, taken in the order of the seventh edition of Gray's Manual.

The data for these reports is compiled chiefly from the Gray Herbarium and the herbaria of the New England Botanical Club, the Connecticut Botanical Society, The Boston Society of Natural History, Yale University and Brown University, supplemented by such other sources as are, from time to time, accessible. In the present report the ranges of some recent segregates, particularly in the genus *Agrostis*, have been made up solely from the material in the first two collections mentioned; these ranges may be modified in some details when it becomes possible to consult other herbaria.

We are, as always, indebted to various members of the New England Botanical Club for cordially given aid, and in this instance especially to Mr. A. H. Norton of the Portland Society of Natural History for a carefully prepared list of stations for Maine grasses. We are also repeatedly indebted to the authorities of the various institutions mentioned above for the privilege of consulting the herbaria under their care.

PRELIMINARY LISTS OF NEW ENGLAND PLANTS—XXXIII.

The sign + indicates that an herbarium specimen has been seen; the sign − that a reliable printed record has been found.

	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
I. ORYZEAE						
Leersia oryzoides (L.) Sw.....	+	+	+	+	+	+
Leersia oryzoides f. glabra A. A. Eaton...	+		+	+		